# CARNIVOROUS PLANT NEWSLETTER

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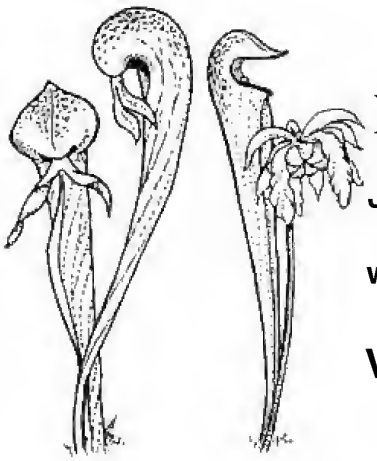

# CARNIVOROUS PLANT NEWSLETTER

**Journal of the International Carnivorous Plant Society**
**www.carnivorousplants.org**

**Volume 39, Number 1**
**March 2010**

Front Cover: *Sarracenia leucophylla* seem to glow in the moonlight. Photo by Barry Rice. Article on page 28.

Back Cover: *Heliamphora sarraceniodes* grown under lights in a terrarium Photo by Brian Barnes. Article on page 26.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Advertisers should contact the editors. Views expressed in this publication are those of the authors, not the editorial staff.

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## Note from the Editor

The March 2010 and June 2010 issues will contain papers that were presented at the 6th Conference of the International Carnivorous Plant Society, June 1-5, 2006.

Stephen Davis
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# 8th ICPS Conference in August 2010!

Carnivora, the Dutch Carnivorous Plants Organization, and the Hortus Botanicus Leiden are proud to host the 2010 International Carnivorous Plant Society Conference in Leiden, The Netherlands from the 6th through the 8th of August 2010. The 9th and 10th of August are reserved for optional excursions.

The conference will take place in and within walking distance of one of the world's oldest botanical gardens, located in the heart of historical Leiden. There will be plant sales by international vendors during the conference and an educational exhibition from the 6th till the 16th of August.

Information can be found on the Carnivora website (www.carnivora.nl) by clicking the conference button on the homepage. The website has general information on the botanical gardens, places to stay, what else to see, and other useful travel information.

Registration, excursion programs and list of lectures are now available on the website.

For general questions, contact us at: icps@carnivora.nl

We hope you will be able to join us in The Netherlands.

— Marcel van den Broek

# Conservation issues at the Watson Pinelands Preserve, Tyler County, Texas

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Keywords: conservation: Texas, Watson Pinelands Preserve, *Sarracenia alata*

Abstract

The Watson Pinelands Preserve (527 County Road 4777, Warren, Texas 77664 (409) 385-7239 or (409) 547-3543) is a 4.8-ha (12-ac) privately owned facility nestled in the Big Thicket of east Texas, and is home to many species of carnivorous plants. Development and maintenance of the preserve as a living record of the rich diversity of East Texas herbaceous and woody plants has not been an easy task, and has had its share of conservation issues as well. This article will discuss some of the many conservation issues that affect the Watson Pinelands Preserve, and what can be done to reduce and/or eliminate some of these effects.

## Discussion

The Watson Pinelands Preserve is a small privately-owned 4.8-ha (12-ac) nature sanctuary in the piney woods of Tyler County, Texas. It is owned and maintained by Ms. Geraldine Watson. Ms. Watson has spent her entire life in the area, and has dedicated the preserve to the memory of her late husband. The preserve serves as a showcase of the floral diversity that was historically found in the area. This entire portion of east Texas has been collectively referred to as the Big Thicket, a region renowned for its rich biodiversity and dense plant growth. Visitors to the Watson Pinelands Preserve can begin their visit in a Longleaf Pine Savannah, traverse a footbridge across a small creek lined with wild native swamp azaleas, *Rhododendron viscosum*, stroll through a fern forest, and finish in a *Sphagnum* bog, all in the space of a few hundred meters.

The preserve has many other plant associations represented as well, including Beech-Magnolia-Loblolly Slopes, Baygall Bogs, and true aquatic habitats like the azalea creek mentioned above and Hyatt Lake, which forms the southern boundary of the preserve. Because of this, visitors to the Watson Preserve can see everything from towering southern magnolias, *Magnolia grandiflora*, American beeches, *Fagus grandifolia*, and longleaf pines, *Pinus palustris*; to diminutive orchids (*Calapogon*, *Habenaria*, *Pogonia* and others), beechdrops, *Epifagus virginiana*, violets, *Viola* sp., and *Sphagnum* sp. Botanical rarities like Scarlet Catchfly, *Silene subciliata*, and several species of fringed orchids, *Platanthera* sp., can be seen at certain times of the year. Of course, a wealth of animals also frequent the preserve, including many species of resident and migratory birds, butterflies, odonates, reptiles, mammals, and other fauna.

The preserve is a serene setting for painting, relaxing, outdoor activities, nature viewing, and other passive recreation. Although privately owned, the preserve has no entrance fees or fencing, making it accessible to visitors at all times free of charge. So for those enlightened individuals who enjoy viewing carnivorous plants in the wild, the preserve is a wealth of visual beauty which can be visited at any time. *Drosera brevifolia*, *D. capillaris*, *Pinguicula pumila*, *Utricularia subulata*, *U. gibba*, and *U. cornuta* can all be seen here at various times of the year, as well as several appreciable stands of *Sarracenia alata*.

As you might have already discerned, there are many issues involved with conserving and maintaining this jewel of east Texas. Some of the most detrimental issues involve direct human problems, but issues can also arise from lack of funding and manpower. For instance, since the preserve is privately owned and charges no admission, funding issues have hindered Ms. Watson's efforts to purchase adjacent undeveloped parcels of land. But after the new millennium, she managed to assemble the funds needed to purchase additional land adjacent to the existing preserve. Land acquisitions can add unique features to the existing preserve, but just as importantly, they can provide buffer zones between the preserve and neighboring developed areas.

One of the first obstacles to overcome on this new land was the elimination of four-wheeler traffic. Numerous four-wheeler trails coursed through and across the new property, and this also

allowed for uncaring individuals to use the property as a dumping ground for all kinds of refuse, up to and including old tires, plastics, and even a few appliances! Of course, this property was privately owned prior to its acquisition by Ms. Watson; but there seem to be no shortage of ignorant individuals who think that the world is their personal dump and playground. It took some time to make sure everyone realized that this was no longer just an undeveloped piece of property; this was now part of the preserve, and that motorized vehicles and dumping were not permitted.

While this land had not been maintained for many years, Ms. Watson's keen eye for the land's potential soon created a vision of a longleaf pine savannah encompassing the existing centrally located spring-fed pool. In the summer of 2003, a group of volunteers met to begin transforming the new property. Initial work involved manually removing undesirable plant species, predominantly Leatherwood, *Cyrilla racemiflora*, and then using fire to remove and retard this and other species. Fire is a commonly used tool at the preserve, but not necessarily during the heat and humidity of an east Texas summer day. Needless to say, volunteers were especially mindful of the risk of heat-related injuries!

Once the area was cleared, a number of mature *S. alata* divisions and other plants were moved from the existing *Sphagnum* bog to this new area. With these optimum conditions, these plants flourished. However, what was amazing to the author was the number of volunteer *S. alata* seedlings which came up as well once the area was opened up. These seeds must have been here for quite some time, waiting for the proper conditions for growth!

Of special importance to naturalists, and especially carnivorous plant enthusiasts, is the introduction of non-native species. As with much of the Gulf Coast region, the Big Thicket has its share of issues with high visibility invasive species such as Chinese tallow, *Triadica sebifera*, Asian species of privet, *Ligustrum* sp., and deep-rooted sedge, *Cyperus entrerianus*. But in 2001 or 2002, some thoughtless individual took it upon themselves to plant a white-topped pitcher plant, *Sarracenia leucophylla*, into the original stand of pure, native Texas *Sarracenia alata* at the Watson Pinelands Preserve. This went unnoticed until 2004, and by this time the *S. leucophylla* plant had cross-pollinated a number of *S. alata*. The author discussed the problem with Ms. Watson, explaining that although this might seem acceptable - since it added a few beautiful red colored inflorescences to the stand, and is a naturally occurring hybrid (*S. areolata*) in other parts of the Gulf Coast - the damage to the genetic purity of this native Texas *S. alata* stand was irreversible. Additionally, the pollen from this *S. leucophylla* and its hybrids might be carried to other pure *S. alata* sites, including those in the Big Thicket National Preserve! Ms. Watson agreed to allow the removal of the non-native *S. leucophylla* and all hybrids, and this work has been conducted each spring, when the hybrids are differentiated by their red or reddish petals, since that time. The removal efforts have many benefits: hybrids are removed, maintaining the pure appearance of the stand, particularly during the spring blooming period; removed plants are offered to interested individuals, in return for donations to the Watson Pinelands Preserve; and the donations are used to help maintain the preserve's boardwalks and other amenities. This is a win-win situation for all.

This hybridization dilemma, though, has also been thought-provoking for me personally in several ways. First of all, if this stand had been represented as a genetically distinct group of plants in a botanical program of some sort prior to the introduction of the non-native *S. leucophylla*, there would have been the opportunity – slim as it may be – to remove all of the *S. alata* and hybrid plants from the site, thereby eliminating any chance of hybrid genetic material to remain. Once the risk of hybrids was removed in this manner, genetically pure specimens from the botanical program could be reintroduced back into the site. This was the impetus for my involvement as the national head grower for the North American Sarracenia Conservancy, a new nonprofit organization whose mission is to "serve as a living record of the taxonomic, morphological and genetic diversity of the genus *Sarracenia* for purposes of conservation and cultivation." More information about this dynamic organization may be viewed at www.nasarracenia.org.

Another hybridization dilemma has been the thought of what effect a minimal amount of *S. leucophylla* genetic material might have on the morphology of specimens of *S. alata*. Flower petal color may usually be deep red in pure *S. leucophylla*; but as the *S. areolata* hybrids continue to outcross with *S. alata* (which usually has pure greenish yellow petals), the petal color becomes less and less red. Eventually, it may be extremely difficult to use simple morphological petal differences to differentiate between pure *S. alata* and the hybrids. Couple this with the fact that the petals in some stands of *S. alata* already show a reddish blush, and there is room for doubt

as to the genetic integrity of some of these plants. *Sarracenia alata* petals with reddish casts have been observed in wild stands in the eastern portion of its range, and in Jasper County, Texas (B. Rice, pers. comm.), where a rare 'windowed' variant of *S. alata* exists. But at what point do you cease to be able to differentiate the genetically pure native *S. alata* from the hybrids? Are these plants with blushed petals and windowed pitchers pure *S. alata*, or a hybrid that has been outcrossed for decades, or even centuries? In the author's opinion, further genetic study is needed to resolve this issue.

Another important issue is that of maintenance. Lack of adequate funds, compounded by the preserve's private status, can cause smaller, less used features of the preserve to go without proper repairs. Many of the bridges and walkways cover only short distances. But several hundred meters of boardwalk can be difficult to maintain, both financially and physically, especially by a widowed woman in her eighties. There are occasional minimal donations of materials and/or labor by private individuals and nonprofit volunteer groups, but this is not sufficient to maintain the boardwalks in a good state of repair at all times, let alone the many other facets of the preserve. Additional funding and volunteers must be found if the preserve is to survive in Ms. Watson's absence.

Winter ice storms and tropical storms can take their toll on conservation efforts as well. Damage to trees caused by ice buildup, and the sustained high winds of tropical systems moving inland, can cause an incredible amount of combustible material to accumulate on the ground. This hampers the ability to conduct prescribed burns, or control those that are conducted, as easily. Too much fuel can be a very dangerous situation. As is the case with many other natural sites containing a large percentage of herbaceous flora, one of the most important methods to control overgrowth is through the use of prescribed burns. Prescribed burns keep large amounts of fuel from building up to dangerous levels, help control or remove unwanted woody growth in sensitive areas, and help turn herbaceous growth and deadfall into nutrients for the next year. At no other time has this been more evident than in the aftermath of Hurricane Rita, which devastated the entire east Texas and western Louisiana area. Scores of trees were downed throughout the preserve, and the amount of deadfall buildup increased significantly. Although the trees were cut into smaller sections and moved when possible, an incredible amount of material was still left behind. This reduced the ability to conduct an efficient burn in 2006, which resulted in an increase in undesirable growth as well. Fortunately, everything is on track for a better prescribed burn in 2007!

Prescribed burns can have some negative effects as well. The sheer heat produced during a burn can kill desirable species as well, and more than one rare tree or herbaceous plant at the preserve has been damaged or even destroyed by the fire's heat. As you might also surmise, it isn't always easy to convince your neighbors that setting the forest on fire is a good thing. The risk of having a fire escape across a fire lane is always present, and the ramifications of such an event can be financially devastating. Wildfires can be caused by escaped burns, and the Watson Pinelands Preserve is surrounded by a densely forested neighborhood. It wouldn't take much to financially ruin this 'diamond in the rough.'

The smoke from a burn can be equally concerning, by causing problems for wildlife, neighbors and even air traffic. Precautions must be taken to make sure the appropriate agencies know that the burn is a planned event, and not a wildfire. The immediate aftermath is not always viewed in a kindly light either, since the appearance of the blackened ground, charred bark on the longleaf pines, and days of smoldering deadfall at the preserve is not necessarily the best way to attract visitors. But for those who understand the burn's purpose and are patient, it doesn't take long for the barren patch of land to begin anew. Each spring produces an astounding visual display of flowers, ferns, and fauna for all to enjoy, and with the wealth of flora represented here, the Watson Pinelands Preserve is sure to give visitors a breathtaking display, no matter what time of year you care to visit.

ADDITIONAL NOTES AS OF THIS PRINTING (March 2010): This paper was presented at the 6th Conference of International Carnivorous Plant Society, June 1-5, 2006, Frostburg, Maryland, USA. As of January 2009, the preserve has obtained its federal 501(c)3 status, and is now known as the Watson Rare Plants Preserve. Prescribed burns are being held annually when conditions permit, and the condition of the preserve's habitats seems as good as ever. However, Hurricanes Rita and Ike were not kind to the manmade structures at the preserve, especially the walking boardwalks in the pitcher plant bogs, and funding for this gem is still minimal. Please consider making a tax-deductible donation to this beautiful corner of the Big Thicket!

## Looking Back: CPN 25 years ago

In June 1984, *Drosera rotundifolia* x *intermedia* was found growing naturally by David Butler during a canoe trip to the Pine Barrens in New Jersey. This anecdote reminds me of the sheer awe I feel when I see carnivorous plants growing in their native habitat. Carnivorous plants are always bigger and more colorful in their native habitat than they are in collections. When I had the opportunity to see *Darlingtonia californica* growing wild in northern California, I was completely unprepared for the enormity of the entire scene. Not only were some of the *Darlingtonia* pushing one meter but the sheer number of individual plants was immense. In some places the *Darlingtonia* fields stretch as far as the eye can see. Now when I look at a cobra lily in a greenhouse it reminds me of the ones I saw in the wild. In short, there's just no way to compare cultivated specimens with naturally growing carnivorous plants. I would recommend to all carnivorous plant enthusiasts that you should set aside some time (maybe just a weekend) to see carnivorous plants that grow natively in your area. It will completely change your perspective.

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# CARNIVOROUS PLANT SYSTEMATICS

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Keywords: systemics, phylogeny, taxonomic composition, geographic distribution, carnivorous plants - general

As can be expected in an ecologically defined group of organisms, carnivorous plants (unlike orchids or cacti) do not constitute one single natural taxonomic unit marked by common descent and close interrelationship. On the contrary, several lines (derived from four different orders of flowering plants) have given rise to carnivorous families or genera (see Figure 1). The classification of at least some carnivorous families is not settled yet, so a somewhat extended discussion of different lines of evidence shall be presented here. A suitable starting point for phylogenetic reconstruction (which alone can lead to a natural system) is the question of geographic origin of the groups investigated. On the other hand, fossilized remnants of phylogenetic ancestors hint at the localization and course of evolution of these groups. Chorological (biogeographic) considerations as well as morphological and chemical comparison are established standard methods in biosystematic research, more recently augmented by data from DNA sequence comparison. Taxonomy at species level or below is the task of botanical monographs and cannot be discussed in detail here. Numbers of commonly recognized species in each group are given in bold face.

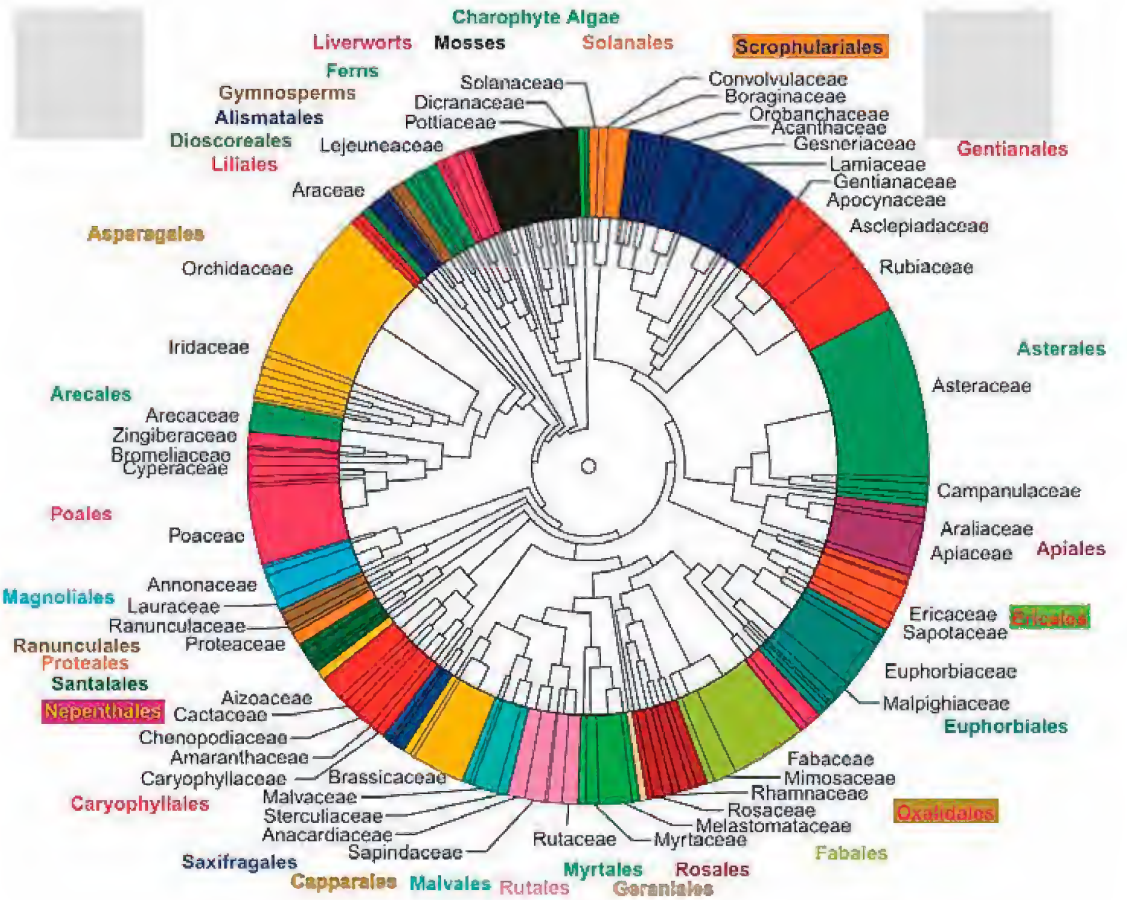


Figure 1: Phylogenetic tree of plant families, sector size approximately corresponding to number of taxa contained. Names of orders containing carnivorous plants are boxed.

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**Rosopsida (true dicotyledons) - Caryophyllidae (pinks, cacti) - Nepenthales** (see Figure 2)

Droseraceae

The Droseraceae, so well known for their widespread representatives in the temperate zone, are one of the most complicated and disputed families of carnivorous plants as far as generic composition and macrosystematic affiliation are concerned. Before a phylogenetic reconstruction can be tried, the generic composition should be established. Here we already meet considerable difficulties. The genus *Byblis*, which was formerly included in Droseraceae (Bentham & Hooker 1862-1883), was shown to have more compelling similarities with Pittosporaceae, and it was grouped as a separate family close to the latter in most recent systems. DNA sequence comparison, not confirming a pittosporacean alliance, does still support ample distinctness between *Byblis* and Droseraceae. Phytochemical evidence quite unambiguously proves *Byblis* to belong to Scrophulariales (*v.i.*). The sub-carnivorous *Roridula* had a fate comparable to *Byblis*, and this genus is also excluded from Droseraceae (usually placed near Ericales) in recent systems. Traditionally, the genera *Drosophyllum* (*v.i.*), *Dionaea* (**1**), *Aldrovanda* (**1**), and *Drosera* (**153**) constituted the Droseraceae of conventional usage. Considerable differences in floral morphology (stamina many *vs.* equal in number to petals and sepals; placentation basal or axial *vs.* parietal) separate *Drosophyllum* and *Dionaea* from *Aldrovanda* and *Drosera*, but the striking similarity between the traps of *Dionaea* and *Aldrovanda* supports at least the inclusion of *Dionaea* into a droseracean core group. This is fully corroborated by pollen morphology (Takahashi & Sohma 1982) and DNA sequence comparison (Williams *et al.* 1994). On the other hand, almost every character beyond carnivory (woody habit, glandular trichomes on the abaxial leaf surface, reverse circinal vernation, pollen in monads, pantoporate, placentation axial) contradicts inclusion of *Drosophyllum* in this core group. In conformity to gene sequence data obtained recently (Meimberg *et al.* 2000), this genus is excluded from Droseraceae and placed closer to *Triphyophyllum* (Dioncophyllaceae). The subdivision of Droseraceae into several families (Chrtek *et al.* 1989) seems unjustified beyond the exclusion of *Drosophyllum*. The exact branching pattern between the three retained genera of Droseraceae is still somewhat disputed, rbcL gene data obtained for a large set of species (Rivadavia *et al.* 2003; see Figure 3) support a sister relationship of *Aldrovanda* and *Drosera* as indicated by floral morphology, *Dionaea* being basal in the family, while an analysis of four genes from a more limited taxa sample (Cameron *et al.* 2002) favours a sister relationship of the snap trap genera *Aldrovanda* and *Dionaea*, *Drosera* being more remote.

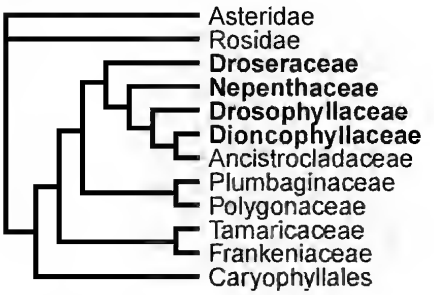


Figure 2: Phylogenetic tree of Nepenthales, carnivorous taxa highlighted

Fossil pollen has been attributed to several genera of Droseraceae. A single record from central European Mid Miocene (called *Fischeripollis*) has been assigned to *Dionaea* (Krutzsch 1970). An interesting series of fossil seeds and even leaves (perhaps traps, if the interpretation is correct) could be established since Senonian for *Aldrovanda* (Degreef 1997; Schlauer 1997a), occurring through large parts of temperate Eurasia (which used to have a warmer climate than nowadays, and which lacks *Aldrovanda* in great parts now) with several different and now extinct species and genera (*Saxonipollis*). This is in very good consonance with the widely scattered distribution of the recent species *Aldrovanda vesiculosa* throughout the old world, resulting from

glacial fragmentation of a formerly continuous range. Droseraceae pollen is represented in the Early Tertiary strata of central Australia (Truswell & Marchant 1986). Mid Palaeocene pollen specimens from Assam (Cherra formation, *Droseridites parvus*, Sah & Dutta 1974) are of uncertain attribution but could also belong to *Nepenthes* (*N. khasiana* being at least geographically a very close recent species, *v.i.*). *Drosera* pollen has been recorded since Lower Miocene from New Zealand (Mildenhall 1980). Miocene pollen (as *Droserapollis* and *Droserapites*) of somewhat uncertain droseracean affinity has been found in Taiwan (Huang 1978). Several finds of Tertiary pollen (since Mid Miocene) from Europe have been assigned to either *Drosera* (*Droserapollis*) or *Nepenthes* (*Droseridites*, Krutzsch 1985). It is, however, unlikely that the recent species of *Drosera* existed in Europe before Pliocene (*v.i.*). Probably, the earlier fossils may be attributed to now extinct lines of Droseraceae or even other families. Anyway, the fossil record of Droseraceae pollen is the richest of any carnivorous plant family, and it testifies a wide distribution at least of the progenitors of *Aldrovanda* since Late Cretaceous.

*Dionaea*, now restricted to the southeastern United States but possibly present in Europe in the Tertiary, shows primitive traits and an obviously relict range, indicative of high phylogenetic age. It may well be that it is the remnant of a very ancient evolutionary line in Droseraceae dating back to the (possibly Late Cretaceous) origin of the family. The geographic location of origin remains obscure, as displacements and extinctions have certainly occurred. *Dionaea* has 2n=30 chromosomes.

*Aldrovanda*, with traps strikingly similar to those of *Dionaea* but in floral morphology very close to *Drosera*, might occupy an intermediate generic position both phylogenetically and geographically. The fossil evidence shows an intense process of diversification throughout the Tertiary period but only one of the emergent species was able to survive the Pleistocene and to occupy the present area of the genus. The place of origin is, like in *Dionaea*, rather uncertain. *Aldrovanda* has 2n=38 chromosomes.

While the phylogenetic roots of the two foregoing genera could have originated in the northern hemisphere, recent species distribution and diversity indicates an Austral accent in *Drosera* (for a taxonomic subdivision, see Schlauer 1996), which is revealed in the occurrence of all apparent palaeoendemics (*D. meristocaulis*, *D. regia*, *D. arcturi*) scattered throughout the southern hemisphere plus tropical America. In this respect, the extant fossil record (especially the European Miocene specimens) is somewhat puzzling. The mentioned, probably most primitive species (with undivided styles and pollen predominantly of primitive operculate types) show a typically Gondwanan distribution (Gondwana is the name of a supercontinent composed of what is now South America, Africa, India, and Australia that existed until approximately 100 MYA). This could reflect a very old (Cretaceous) age of the genus, and therefore, of the whole family, dating back to stages of tectonic development when South America, Africa, and Australia were in closer proximity to each other than nowadays. The primitive status of *D. regia* is fully confirmed by gene sequence similarity (Williams *et al.* 1994; Rivadavia *et al.* 2003).

*Thelocalyx* (**2**), a group of probably higher advancedness but uncertain descent (marked by a uniformly pentamerous gynoecium and pollen of a unique intermediate type with 20-30 pores

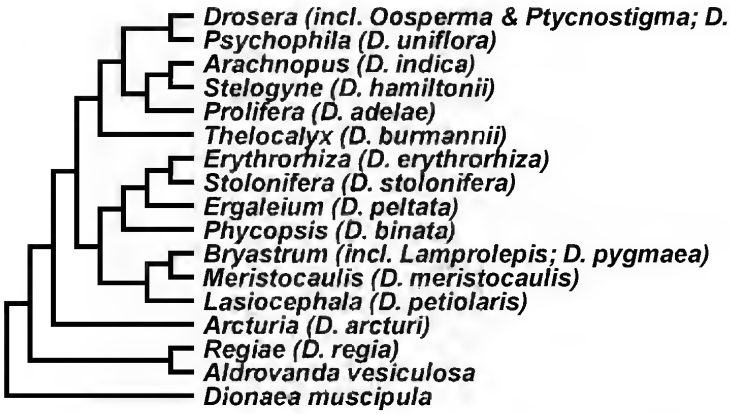


Figure 3: Phylogenetic tree of Droseraceae

scattered on the proximal face), shows a similarly disjunct distribution with one species (*D. burmannii*) in the tropics of Asia and Australia and the other (*D. sessilifolia*) in tropical South America. Genetic analysis (Rivadavia *et al.* 2003) places *Thelocalyx* close to the derived (and widespread) clades characterized by three basally split styles.

Judging from recent species, Australia is a (perhaps secondary) center of diversity of the genus (Schlauer 2000), and most of the more recent lines of *Drosera* can be assumed to have originated here. With the remarkable exception of Coelophylla, all of them share derived pollen types with a single proximal pore.Two predominantly Australian groups are composed of species with corms (subgen. *Ergaleium*, **40**, only one line of which, consisting of the variable *D. peltata*, leaving Australia to reach New Zealand and Asia, and the closely related species *D. insolita* being rather isolated in Africa) and of species that form tight stipule clusters and propagate by asexual gemmae from transformed leaves (*Bryastrum*, **30**, of which only *D. pygmaea* reaches also New Zealand). These two very distinct groups obviously show adaptation to a dry climate, which seems a logical consequence of northward moving Australia, thereby entering the subtropical desert belt. Both groups are involved in vivacious speciation processes, which is reflected by frequent cases of sterility (probably caused by hybridogenic origin from incompatible parent species) and morphological overlap (reticulate character distribution) especially in southwest Australia, the core of species diversity. A fundamental genetic instability due to diffused centromeric chromosome organization (Hoshi & Kondo 1998a & b) is possibly facilitating diversification by chromosome loss, fragmentation, and fusion. Chromosome counts are consequently somewhat puzzling in these groups. *Bryastrum* includes species with complements of 6, 7, 8, 10, 12, 14, 16, 18, 20, and 28 chromosomes, and most notably for the disjunct *D. pygmaea* counts of 2n=32 and 64 have been obtained. *Ergaleium* contains species with 14, 20, 24, 26, 28, 28, 30, 32, and 40 chromosomes.

On the other hand, the northernmost portion of Australia entered the tropical humid zone only recently, and some tropical members of *Drosera* may either have invaded this new habitat from the north (New Guinea or the Asian mainland: perhaps sect. *Arachnopus* - **1**, and *D. burmannii*, belonging to Thelocalyx, but *cf.* discussion on origins of Asian species below) or they may have originated in north Australia (probably subgen. *Lasiocephala* - **15**, and sect. *Prolifera* - **3**, both most diverse in Australia and with obviously Australian affinities). *Lasiocephala* shows interesting similarities to *Bryastrum* (including deciduous leaf laminae, a possible homology to the gemmae that are likewise developed from laminae), from which it differs by its divided styles. Chromosome counts confirm the affinity of the somewhat disputed D. banksii (2n=12) to the core of sect. *Lasiocephala* (x=6), and this count is also known from *Bryastrum*.

Some Australian groups (*e.g. Coelophylla* - **1**, with an apparently primitive pollen type with 15-20 pores arranged in a circle on the proximal face, and *Stelogyne* - **1**, with connate styles) take unclear intermediate positions, indicating possible links between the larger evolutionary lines, the former being closer to the Australian clade containing *Ergaleium* and *Bryastrum*, the latter approaching the northern clade containing sect. *Drosera*. *Phycopsis* (**1**), represented only by the polymorphic *D. binata*, stands at the base of the line leading to *Ergaleium*, with which it shares the plurifid styles, pollen morphology and DNA sequence homology, being different by the possession of stipules and by the lack of corms. DNA sequence comparison (Williams *et al.* 1994; Rivadavia *et al.* 2003) and phytochemistry (Culham & Gornall 1994) confirm an affinity of *D. binata* to subgen. *Ergaleium*.

In south Africa a side branch still evidently related to the more recent lines of subgen. *Drosera* developed the roots into thickened storage organs, enabling the representatives to survive in seasonally drier habitats, a remarkable convergence to the corms formed in subgen. *Ergaleium*. However, the overwhelming majority of the African and American species are constituted by the derived sections of subgen. *Drosera* (together **48**) which most probably also had a Gondwanan origin but not necessarily in Australia. The species are closely interrelated, and species limits are not always clear. Members with different seed morphology are interfertile, and they all share the chromosome base number of x=10. Hybridization and introgression may account for some of the trouble in determining species in south Africa and elsewhere, and several taxa are probably of hybridogenic origin. Recent migrations of members of both sections across the American continent and a rather recent spread from there to temperate Eurasia are obvious. Much or all of the area of the three recent Eurasian species (*D. intermedia*, *D. rotundifolia* and *D. anglica*, all of which also being present and widespread in North America) was probably conquered during or

after Pleistocene, and *Drosera* still behaves like a foreign element in the Eurasian flora, restricted to very specialized, typically postglacial habitats. In this context it is notable that the species now distributed throughout tropical and subtropical Asia (*D. burmannii*, *D. peltata*, *D. indica*, and *D. spatulata*) are all known from Australia (with the exceptions of an odd occurrence of *D. rotundifolia* in New Guinea and the recently described *D. oblanceolata*, which is probably a recent derivative of *D. spatulata* endemic to subtropical China). So the whole *Drosera* flora of Asia may be composed of originally North American (temperate) and Australian (subtropical and tropical) elements that have possibly invaded Asia only relatively recently from the northeast (possibly *via* a Behringian route) and from the east (possibly *via* New Guinea). Two of the Asian species (*D. indica* and *D. peltata* replaced by its vicariant *D. insolita*, *v.s.*) are also represented in tropical and subtropical Africa, which would be a logical continuation of a westward migration.

The problems sketched during the discussion of generic composition are continued in macrosystematic considerations. Almost every system proposed has an individual "solution" for the placement of Droseraceae. A great deal of the difficulties was caused by the successive blurring of familial characteristics by inclusion of *Dionaea* or even *Drosophyllum*. Early systems saw an affinity (*via Parnassia*) to *Crassulaceae* and *Saxifragaceae* (Bentham & Hooker 1862-1883), of which at least the affinity to *Parnassia* is adopted even by more recent approaches (Dahlgren 1980; Young 1982; Thorne 1983). The Sarraceniales problem (Melchior 1964, and successors) will be sketched under Sarraceniaceae (*v.i.*), and such a grouping, at least one of Droseraceae close to Sarraceniaceae is no longer maintained in recent systems. Some proximity to Nepenthaceae is conveyed by tetrad pollen and the fact that both families form acetogenic naphthoquinones, and the latter are present also in the Dioncophyllaceae, Ancistrocladaceae, Plumbaginaceae, all of which are members of Nepenthales in a revised circumscription (Schlauer 1997b). DNA sequence comparison favours a grouping of Droseraceae close to a Nepenthaceae + (Drosophyllaceae + (Dioncophyllaceae + Ancistrocladaceae)) clade (Meimberg *et al.* 2000). Because of the obvious similarities between the trapping leaves and in DNA sequence of *Drosophyllum* and *Triphyophyllum* (Dioncophyllaceae), a close affinity between these two genera (which are fundamentally different in the flower, however) seems possible. Parietal placentation, at least in *Aldrovanda* and *Drosera* has suggested affinity to Violaceae and/or Ochnaceae (DeCandolle 1823-1873; Wettstein 1935), but was dismissed as being decisive in later systems. All in all, it can be stated that in spite of a majority of traditional systems favouring proximity to Parnassiaceae, Crassulaceae, and Saxifragaceae (all being "rosid" families), the systematic position of the Droseraceae can now rather safely be allocated in Caryophyllidae.

Dioncophyllaceae

This family (**3**) is the only one which contains only one carnivorous genus among non-carnivorous ones. In early systems it was included in Flacourtiaceae (Dalla Torre & Harms 1900-1907) and has not been altered in composition since its segregation (Airy Shaw 1952). The three genera are closely interrelated and exclusively tropical west African. *Habropetalum* and *Triphyophyllum* are sympatric but the latter is apparently more closely related to the disjunct *Dioncophyllum* (Meimberg *et al.* 2000). The feature of the fruits opening before seed maturity (paralleled to some degree in *Anchietea* and *Decorsella*, Violaceae), the seeds dramatically surpassing the ovary in size, is so unique in the plant kingdom that the family is readily characterized.

Parietal placentation was assumed (together with the striking fruit similarities) to support an affinity with Violaceae and Flacourtiaceae (Hutchinson 1973; Cronquist 1981; Takhtajan 1980). A position near Hypericaceae-Kielmeyeroideae and Nepenthaceae was discussed (Airy-Shaw 1952). The placement between Ochnaceae and Strasburgeriaceae (Melchior 1964) or more generally speaking, in Theales (Dahlgren 1980; Thorne 1983) also suggests a "dilleniid" affiliation ("Dilleniidae" in the sense applied in older classifications - incl. *e.g.* Theales and Malpighiales - cannot be upheld because the group was founded on artificial characters, and the component families belong to many independent lineages of dicotyledons, *e.g.* Rosidae, Ericidae, Asteridae). However, convincing similarities in pollen morphology and anatomy, and the common and unique presence of acetogenic naphthylisoquinoline alkaloids in both families leaves little doubt that Ancistrocladaceae (**22**, distributed throughout the tropics from west Africa to southeast Asia, but with notable disjunctions) are the most closely related sister group of Dioncophyllaceae (Dahlgren 1980). This was more recently also confirmed by DNA sequence comparison, indicat-

ing also a close relationship to *Drosophyllum* (Cameron *et al.* 1995). Fossils from the Eocene of Raitschikha in the Amur district have been interpreted as Dioncophyllaceae seed (Fedotov 1982). If the assignment was accurate, this would indicate that the west African speciation of a formerly tremendously more widespread family must have taken place in relatively very recent time, while the family was much older. Such a situation could scarcely be explained by a simple chorological theory, and serious doubts about the identity of the fossil remain. *Triphyophyllum* has 2n=24 or 36 chromosomes, depending on the source.

Drosophyllaceae

*Drosophyllum* (**1**) is isolated both geographically (Portugal, southwest Spain, northwest Morocco) and systematically (*v.s.*). Although it is now placed rather remote from Droseraceae, it was originally described as a species of *Drosera*. Many different lines of evidence (*v.s.*) place it next to a clade containing Dioncophyllaceae and Ancistrocladaceae, both of which are well represented in tropical west Africa. The present disjunction was probably caused by the rather recent expansion of the Saharan desert, in which neither of the families can survive. With 2n=12 chromosomes and its apparently likewise ancient relatives, *Drosophyllum* is probably an old relict (palaeoendemic) that may have originated in subtropical regions of Africa long before the expansion of the desert belt.

Nepenthaceae

This family contains only the genus *Nepenthes* (**90**), the circumscription of which has never presented taxonomists with difficulties because of the unique pitcher traps formed in all known species. Its subgeneric classification, on the other hand is one of the most complicated tasks in plant taxonomy, and the delimitation of species or natural species groups remains difficult. As far as it is known, all species are readily interfertile (sharing the uniform chromosome number of 2n=80; Heubl & Wistuba 1995), which has also resulted in numerous horticultural hybrids. The interrelationships of the numerous described species (summarized in Danser 1928 and Jebb & Cheek 1997) have to be established by future research. So this will not be discussed in much detail here (for a summary of infrageneric classification until that date see Harms 1936). Genetic studies (Meimberg *et al.* 2001; see Figure 4) confirm a basal position of the western species (from Madagascar to Sri Lanka and the Khasi Hills in northeastern India), monophyly of a group of New Guinean species, of the relatives of *N. tentaculata* (Borneo and Sulawesi), and of a clade containing the moderately derived species with appendages on the lower surface of the lid (*Regiae*, Borneo, Philippines, Sulawesi, New Guinea). The bulk of described species (which apparently constitute

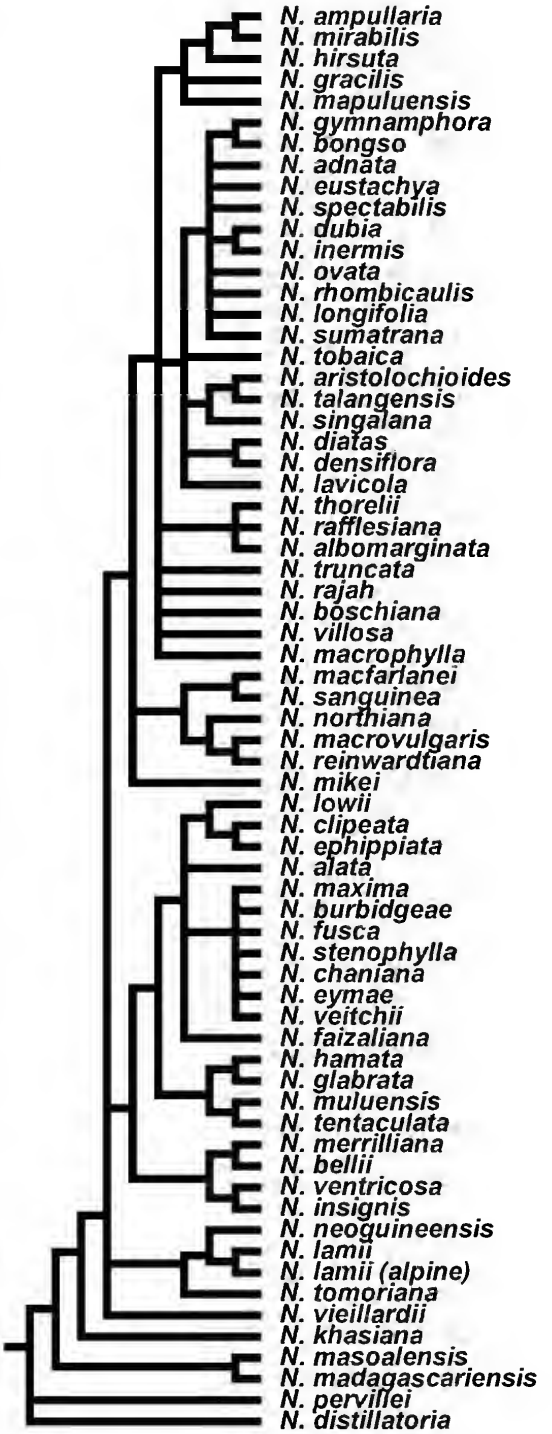


Figure 4: Phylogenetic tree of Nepenthaceae

the most derived clade of the genus, mainly from Borneo and Sumatra) still have poorly understood mutual relationships. Possibly of evolutionary significance is the fact that pollen originally assigned to Droseraceae (*Droseridites*) from the Kerguelen islands has been tentatively transferred to *Nepenthes* more recently (Krutzsch 1985). In this context *Droseridites parvus* from the Mid Palaeocene of Assam (Sah & Dutta 1974) should be considered as possible *Nepenthes* pollen. Fossil pollen assigned to *Nepenthes* has been discovered in the Mid Miocene of north Borneo (Anderson & Müller 1975), and its presence here (a center of recent diversity, Schlauer 2000) is not surprising. But the assignment of European Tertiary pollen to the same genus (Krutzsch 1985) is at least as puzzling as the dubious *Triphyophyllum* seed from Siberia (*v.i.*, recalling to some extent a similar discrepancy between fossil record and present distribution in Dipterocarpaceae and Clusiaceae). The total recent range of the family shows pronounced indicators of an east Gondwanan origin with strong tropical preferences, covering Madagascar (*N. madagascariensis* and *N. masoalensis*), the Seychelles (*N. pervillei*), Sri Lanka (*N. distillatoria*), east India (Khasi Hills, *N. khasiana*, the only species north of the tropic of cancer!), continental and insular southeast Asia (most species), north Australia (only the widespread (*N. mirabilis*), New Guinea (several species) and New Caledonia (*N. vieillardii*). The fact that Nepenthaceae are absent from Africa (although the light seeds would seem capable of long distance dispersal) but present in extratropical India could indicate a time of origin at an early stage of the continental drift which has resulted in the present fragmentation of former Gondwanaland. This would mean that Nepenthaceae belonged to very early angiosperms. However, also other theories (*e.g.* integrating the European Tertiary pollen finds) are conceivable.

The macrosystematic placement of Nepenthaceae used to be subject to dispute similar to the situation in Droseraceae. While in the latter family its puzzling heterogeneity makes decisions difficult, Nepenthaceae are very uniform but the combination of primitive and derived characters (dioecious habit, perianth segments 4 without distinction between sepals and petals, stamina fused in a column, pollen in tetrads, placentation axial) isolates the family far from any hypothetical ally. This could, besides chorology, be a further indication of great phylogenetic age of the family as a whole (whereas some specialized endemic species seem to be rather young). Very indicative of the mentioned problems is the classification near Podostemaceae and Rafflesiaceae (Bentham & Hooker 1862-1883), both families have likewise undergone fundamental transformations and reductions in floral morphology but the similarities are probably of a convergent nature. Even in subsequent systems (Wettstein 1935; Hutchinson 1973) Nepenthaceae were grouped with other assumedly primitive families. The inclusion of Nepenthaceae in the traditional Sarraceniales seems to be as artificial as in the case of Droseraceae (*v.s.*). An affinity to Droseraceae seems to be supported by pollen in tetrads and presence of naphthoquinones in both families, almost all other features remaining contradictory. Some recent systems place Nepenthaceae near Dioncophyllaceae (Dahlgren 1980; Young 1982; Thorne 1983). The latter is supported by several additional data, but the affinity is at the most rather loose, and the divergence must have taken place at an early stage of the evolution of the two families, *i.e.* possibly at an early stage of angiosperm evolution. A caryophyllid placement of the family is confirmed by DNA data (Meimberg *et al.* 2000).

**Rosidae (dicotyledon core group) - Oxalidales** (see Figure 5)

Cephalotaceae

This monotypic family is endemic to southwest Australia. No fossils have been attributed to Cephalotaceae, and no recent taxon was brought into close proximity of this family on morphological grounds. The precise place and time of origin are unknown. Thus, it can only be guessed to have been somewhere in Australia in habitats with ecological conditions comparable to the present range. Some hints can be expected from the macrosystematic position of *Cephalotus* (**1**). Despite some reduction in the number of ovules per carpel (leading to basal placentation), a great consent among various authors can be found as to a placement of Cephalotaceae close to Crassulaceae and Saxifragaceae (common traits being herbaceous habit, carpels distinct or basally connate,

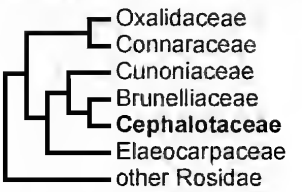


Figure 5: Phylogenetic tree of Oxalidales and Cephalotaceae

tapering into the style, placentation axial or submarginal or basal, seeds with endosperm, flowers hypogynous or perigynous, actinomorphic), the similarities especially in the gynoecium being decisive. A grouping of Cephalotaceae quite remote from *Saxifraga* and *Crassula* but close to *Platytheca* (Tremandraceae), *Ceratopetalum* (Cunoniaceae), *Eucryphia* (Eucryphiaceae), or *Oxalis* (Oxalidaceae), as suggested by DNA sequence comparison (Albert *et al.* 1992) came, therefore, as a great surprise. A more recent study (Bradford & Barnes 2001) identifies *Brunellia* (Brunelliaceae, South America) as the closest relative of *Cephalotus* (a grouping already suggested by Engler 1897). In most of the recent systems, some of these latter genera show at least some proximity to Saxifragales, but this grouping is not supported by genetic data. Anyway, a position at the base of the moderately derived "rosid" dicotyledons, and therefore originating from a line of rather old age (at least since Early Tertiary, possibly since Cretaceous) can be expected for Cephalotaceae. Given a northward movement of Australia since the supposed time of origin, the place of origin could have been situated in nowadays more northern regions of Australia (which are nowadays too arid for *Cephalotus*), where it most probably emerged from an early rosid, non-carnivorous progenitor. The development of the pitcher is unique among carnivorous ascidia, the lid being an excrescence of the base of the lamina (transversal zone of a peltate leaf), the rim being homologous to the apical leaf margin. Thus, any grouping together with other pitcher plants (*cf.* Wettstein 1935) would be based on convergence rather than true phylogenetic relationship. All existing evidence indicates a very isolated position of Cephalotaceae with respect to other carnivorous plant families. *Cephalotus* has 2n=20 chromosomes.

**Asteridae (sympetalae, dicotyledon crown group) - Ericales** (see Figure 6)

Sarraceniaceae

The Sarraceniaceae are at present a purely American family of high homogeneity, the holophyletic and monophyletic nature of which has never been doubted. The division into Heliamphoraceae (including only *Heliamphora*) and Sarraceniaceae *s. str.* (including *Sarracenia* and *Darlingtonia*) does reflect the relative distinctness between South and North American genera (Chrtek *et al.*, 1992) but it does not seem appropriate to represent this by such a grave formal change (only a shift of ranks without significant taxonomic information). Morphological features are distributed in a reticulate fashion among the three genera so the course of evolution has been inferred in several different ways (Schnell 2002; Maguire 1978; Steyermark 1984). The geographic origin of the Sarraceniaceae would appear to be located in America. A recent fossil find from the Cretaceous of the Liaoning formation in China (Li 2005) assigned to an ancestral genus of Sarraceniaceae and in some respects reminiscent of *Heliamphora* pitchers does, however, suggest an alternative scenario. Following this hypothesis, Sarraceniaceae would be the descendants of a subtropical Arcto-Tertiary element that is characteristic for many East Asian and East North American genera and families. While most of these disjunct taxa are more diverse in Asia than in America, the opposite would apply to Sarraceniaceae with no known recent Asian representatives. A trend of increasing complexity of the trapping devices in the order *Heliamphora* (**6**) → *Sarracenia* (**8**) → *Darlingtonia* (**1**) can be formulated, a simple marker of which being the increasing specialization of the pitcher mouth and the apical pitcher appendage (lid). This trend is not followed completely by floral morphology. *Heliamphora*, the apparently most primitive genus by foliar morphology, shows remarkable adaptations to specialized insect pollination, not paralleled by *Darlingtonia* or *Sarracenia*, which seem more advanced on the basis of leaf complexity. The chromosome numbers (2n=42 in *Heliamphora*, 26 in *Sarracenia*, and 30 in *Darlingtonia*) do likewise not follow the trend

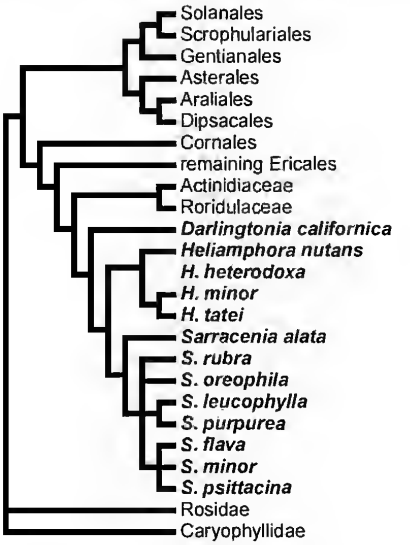


Figure 6: Phylogenetic tree of Ericales and Sarraceniaceae

observed in foliar morphology. Being restricted to the Guyana Highlands, which are home to several ancient relicts (the mountains were exposed to erosion since the Cretaceous without significant folding or displacement), *Heliamphora* seems to indicate descent from a point close to the origin of the family. This was also deduced from comparative wood anatomy (DeBuhr 1977). *Sarracenia*, distributed in the temperate eastern part of North America from the Gulf coast to Canada, shows the largest area of distribution in the family. This *i.a.* reflects a much broader ecological amplitude indicative of a more derived descent. Finally, *Darlingtonia*, restricted to the Cascade Range in north California and adjacent southern Oregon, is probably a palaeoendemic element of this comparatively young (the most recent Cascadian orogeny occurred in Late Tertiary) mountain system. The pitcher of *e.g. S. psittacina* is remarkably similar to the one of *Darlingtonia* (while the flowers are rather different). Recent genetic investigations (Bayer *et al.* 1996) place *Darlingtonia* as a sister clade to a branch containing *Heliamphora* and *Sarracenia*, making a descent of *Darlingtonia* directly from *Sarracenia* unlikely if the latter is derived from *Heliamphora*, as generally assumed.

While it seems possible to sketch the evolution within Sarraceniaceae, the task of finding macrosystematic linkages of the family is much more difficult. The apparently primitive traits in floral morphology (*e.g.* a frequently pleiomerous androecium) have led some authors to assume a relationship with Papaveraceae (Bentham & Hooker 1862-1883; Takhtajan 1980; Rouleau 1981). The carnivorous habit was the reason for inclusion of Sarraceniaceae in a variously remodelled order Sarraceniales/Nepenthales together with Nepenthaceae (also with pitcher traps, the apparent homology of which to *Sarracenia* pitchers being erroneous, however) and Droseraceae (entirely unrelated and different in almost every respect, apart from carnivory). This obviously paraphyletic assemblage enjoyed a remarkable longevity in systematic literature (Melchior 1964; Cronquist 1981). It was even argued that some homology existed between the different trapping devices (Markgraf 1955) although this had been clearly demonstrated not to be the case by earlier work (*e.g.* Troll 1939). Probably a "relict" of this tradition is the inclusion of Sarraceniaceae in or near Theales as a sister group of Lecythidaceae, Ochnaceae, and Hypericaceae, another sister being Nepenthaceae (Young 1982; Thorne 1983). Rather odd is the classification of Sarraceniales (together with Droseraceae but excluding Nepenthaceae) as a sister order of Podostemales, derived from a saxifragalean origin (Hutchinson 1973). Other recent classifications group Sarraceniaceae close to the Ericales, and Cornales on the basis of phytochemical similarities (Dahlgren 1980). Interestingly, DNA sequence comparison seems to support the placement near Ericales together with the likewise phytochemically similar Roridulaceae (Albert *et al.* 1992).

No clear affiliation can be proposed from the cited data except for a possible but loose affinity to Roridulaceae and Actinidiaceae (Schönenberger *et al.* 2005). This causes the question of age to remain essentially open as well. However, it seems evident that with the exception of *Sarracenia purpurea*, no taxon of Sarraceniaceae was involved in recent range extension, and the present genera represent relicts of a formerly more continuous or dynamic familial range. It has been pointed out that *Heliamphora* could not have migrated for the considerable distances which separate it from the other genera nowadays (Maguire 1978). But this would not have been necessary if the progenitors of the recent genera developed in northern (tropical) South America, *Heliamphora* remaining dependent on the conservative conditions of the Guyana Highlands, while *Sarracenia* was more or less able to migrate for long distances (a recent proof being the mentioned *S. purpurea*) and to cope with a seasonal temperate climate (depending on the species; marked differences in this respect can be seen within the genus even nowadays). It is more difficult to explain the origin of *Darlingtonia*, a montane palaeoendemic with features typical for Tertiary relicts. Perhaps, the South American progenitors were first separated ecologically (by sympatric differentiation), and with the onset of climatic changes this resulted also in geographic separation.

**Asteridae - Scrophulariales (Lamiales, Bignoniales) (Bremer *et al.* 2002; Müller *et al.* 2004; Olmstead *et al.* 2001**; see Figure 7)

Byblidaceae

This family contains only the genus *Byblis* (**6**). The sub-carnivorous genus *Roridula* (**2**), which has formerly been grouped within *Byblidaceae* (Hutchinson 1973; Cronquist 1981), is now usually regarded an independent family. In this strict sense, Byblidaceae inhabit Australia and New Guinea. Fossil seeds found in the Tertiary of Australia have been attributed to Byblidaceae

(Conran & Christophel 2004). Like in Cephalotaceae, an Australian origin can thus be assumed. The recent distribution (largest diversity in Northern Australia) may, however, indicate a somewhat more tropical preference (*i.e.* a place of origin somewhat closer to the equator). Byblidaceae have been associated with Droseraceae in early systems (Bentham & Hooker 1862-1883), the main reason being the carnivorous habit by virtue of adhesive traps. But later on, the family has almost unanimously been placed close to the Pittosporaceae (especially to the genus *Cheiranthera*, which shares the irregular corolla and poricidal anthers with *Byblis*) or Tremandraceae (Hutchinson 1973). This or at least a "rosid" classification has been corroborated by several lines of evidence, *e.g.* wood anatomy (Carlquist 1976), and palynology (pollen tricolporate). However, DNA Sequence comparison (which corroborates a separation from Roridulaceae and placement of this latter family near Ericaceae) indicates a closer affinity of Byblidaceae to Scrophulariales or Solanales (Albert *et al.* 1992; Conran & Dowd 1993). Compelling proof for a Scrophularialean placement comes from phytochemistry: Acteoside, a specific caffeic acid glycoside, has been identified as a characteristic chemical marker of Scrophulariales (Scogin 1992), it is present in all examined families (more than 140 genera) of this order, and only four incidences are known outside the order (in Asteraceae, Campanulaceae, Cucurbitaceae, and Magnoliaceae). The detection of acteoside in *Byblis* (Budzianowski *et al.* 1997; Schlauer *et al.* 2004) readily places the family in Scrophulariales. Flower structure (slight asymmetry, only basal sympetaly) suggests a position near the base of the order. The quite different morphology of the glandular hairs and the very weak sympetaly of *Byblis* do not support speculations about close affinities to *Pinguicula* (belonging to the same order) beyond pure convergence. Caryology is not uniform within *Byblis* (2n=14, 16, 18, 24, or 32 depending on species).

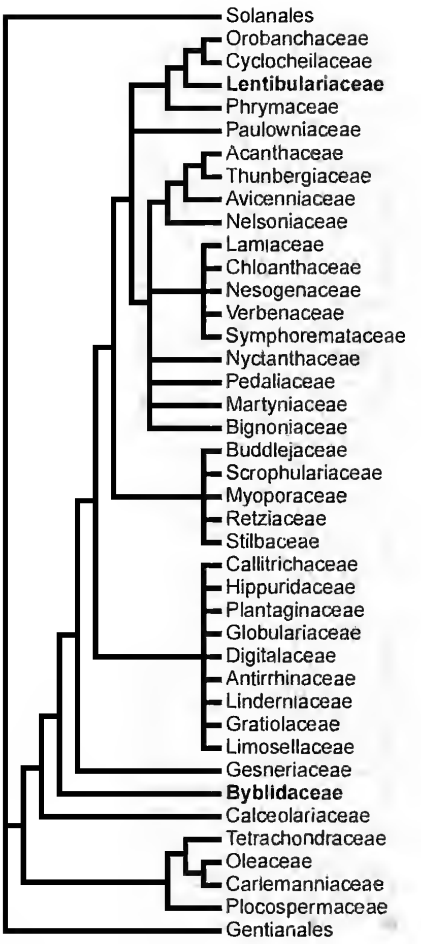


Figure 7: Phylogenetic tree of Scrophulariales, carnivorous taxa highlighted

Lentibulariaceae

Even though the three genera included in this largest family of carnivorous plants have rather different trapping mechanisms, there is no doubt that they all belong to the same family which is monophyletic and holophyletic without non-carnivorous members ("The taxonomic limits of the Lentibulariaceae are not in question", Cronquist 1981: 975). Thus, speculation on paraphyly (Molau 1990) is essentially unjustified. The compelling evidence does, however, not stem from the common trait of carnivory. It can completely be deduced from floral morphology. The lentibulariacean flower is of a spurred personate type. This places the family readily in the order Scrophulariales. But unlike Plantaginaceae-Antirrhineae, the androecium is reduced to the two anterior stamens, indicating a possible closer relationship to Scrophulariaceae-Gratioleae, where this trait is common. The mentioned synapomorphies of Lentibulariaceae would already be sufficient for familial delimitation but the picture is completed by the universal (within Lentibulariaceae) and unique (within Scrophulariales) reduction of the ovary septum so that placentation becomes free-central (the originally two carpels still reveal themselves in the two remaining stigma lobes). The placentation type has even been argued to suggest a placement near

Primulaceae (DeCandolle 1823-1873), but the distinctive corolla features are rather prohibitive of such. No recent system has positioned Lentibulariaceae outside Scrophulariales ("It is generally agreed that the Lentibulariaceae are derived from the Scrophulariaceae", Cronquist, *l.c.*). A position within Scrophulariales is also supported by gene sequence homology (Albert *et al.* 1992) and by the presence of acteoside (*v.s.* under Byblidaceae). The internal phylogeny of Scrophulariales is not well understood yet, but a descent of Lentibulariaceae from Scrophulariaceae or a related family is not at variance with non-morphological data. The fossil record of Lentibulariaceae is rather poor, and only pollen of aquatic *Utricularia* species (*i.e.* probably the most derived line in the family) is known - doubtfully since Oligocene from Cameroon (*Psilostephanocolporites minor*, Salard-Cheboldaeff 1978), and rather certainly since Upper Miocene from Mexico (Graham 1976), Senegal (Medus 1975), and Georgia (Cohen 1975). From increasing trap complexity and decreasing vegetative organization, a progressive arrangement *Pinguicula* (calyx lobes 5, true roots and leaves present) ➔ *Genlisea* (calyx lobes 5, roots missing, leaves present) ➔ *Utricularia* (calyx lobes 2 by coalescence, roots and leaves replaced by specialized stolons) seems plausible. The origin of the family should be sought where all three recent genera occur together, *viz.* in Central America (Guatemala to Colombia). Close to this probable center of origin, also the center of diversity of the assumedly most primitive genus, *Pinguicula*, can be located (Mexico, Caribbean, North American Gulf coast, Schlauer 2000).

*Pinguicula* (**75**) is widespread throughout the holarctic floristic kingdom with but few (and rather young) species. It also reaches Patagonia *via* the Andes, where few closely interrelated and typically vicariant species can be found. *Pinguicula* can be postulated to have originated in Early to mid-Tertiary. The genus has developed the extant subgenera except subgen. Pinguicula, which is of predominantly European origin (*v.i.*), in the new world before it spread to increasingly temperate, and finally arctic latitudes to the north. Another line can be postulated to have entered South America not until relatively recently (Pliocene) when the isthmus of Panama became a land bridge to central America again (having been submerged for the most time of the Tertiary). An (obviously secondary) center of diversification developed since Miocene in the high mountain regions surrounding the European Mediterranean (Casper 1966). From this, the nowadays most widely spread species (*viz. P. vulgaris*) and perhaps *P. alpina* have originated. *P. vulgaris* reached Siberia and North America, being replaced around the Pacific Ocean by the closely related *P. macroceras*. *P. alpina* inhabits the European Alps, Scandinavia, Siberia, and the Himalaya. Thus, the circumboreal prevalence of the generic range is a recent feature and not indicative of the generic origins. On the basis of floral morphology, four distinct lines were distinguished within *Pinguicula*: subgen. *Isoloba* (sections *Isoloba*, *Cardiophyllum*, *Agnata*, *Discoradix*, *Homophyllum*, and *Heterophyllum*, **28**, mainly central and subtropical North America, few species in Atlantic and Mediterranean Europe), subgen. *Temnoceras* (sections *Temnoceras*, *Ampullipalatum* , *Micranthus* , and *Nana* , **15**, central and Andine South America, few species from Europe to Siberia, reaching the Himalaya, north Korea, Japan, and Kamchatka), *Orcheosanthus* (originally described as a section within subgen. *Pinguicula* but obviously distinct, **21**, central America), and subgen. *Pinguicula* (only sect. *Pinguicula*, **11**, Eurasia, Mediterranean, and temperate North America). Chromosome counts only partially reflect the developments within the genus. Base numbers are x=8 (characteristic for subgen. *Pinguicula*, and subgen. *Temnoceras* but also found in *Orcheosanthus*) and 11 (common in *Isoloba* and *Orcheosanthus*). The apparently primitive *P. lusitanica* (subgen. *Isoloba*) has 2n=12, the lowest known count in the genus.

Genetic work (Cieslak *et al.* 2005; Kondo & Shimai 2006; see Figure 8) places the subtropical North American and European Representatives of *Isoloba* together with the Andine species of *Temnoceras* (*Ampullipalatum* ) in a monophyletic clade at the base of the genus. The more derived clade is split between subgenus *Pinguicula* (without sect. *Orcheosanthus*) and all remaining species (central American/Caribbean species of *Isoloba*, *Temnoceras*, and *Orcheosanthus*, and the relatives of the Eurasian *P. alpina* - *Micranthus* & *Nana*). It thus appears that chorology is much more indicative of the phylogeny of the genus than is floral morphology. It is, however, surprising that none of the basal species occurs in central America (the place with most present diversity in the genus).

The small and highly uniform genus *Genlisea* (**20**) is confined to the tropics of America and Africa (including Madagascar, Fischer *et al.* 2000), probably with a center of origin close to or

south of the one of *Pinguicula* (*viz.* central or northern South America), where still local centers of diversity are present. However, the seemingly more primitive species (sharing the laterally or longitudinally bivalvate capsule with *Pinguicula*), classified (Fromm-Trinta 1977) as sect. *Tayloria* (**3**), are nowadays confined to Brasil (NB: it is possible that both recent dehiscence types in this genus are of a derived nature, *cf.* also the various dehiscence types present in *Utricularia*, displaying parallelism and convergence). The remaining species are marked by circumscissile capsules and are classified as sect. *Genlisea* (**17**). The present range of sect. *Tayloria* may reflect a relict nature (if this section was really the more primitive one). The tropical Afro-American distribution is suggestive of a rather old age of the genus, and overall morphology points at an early divergence from the common ancestors with *Pinguicula*.

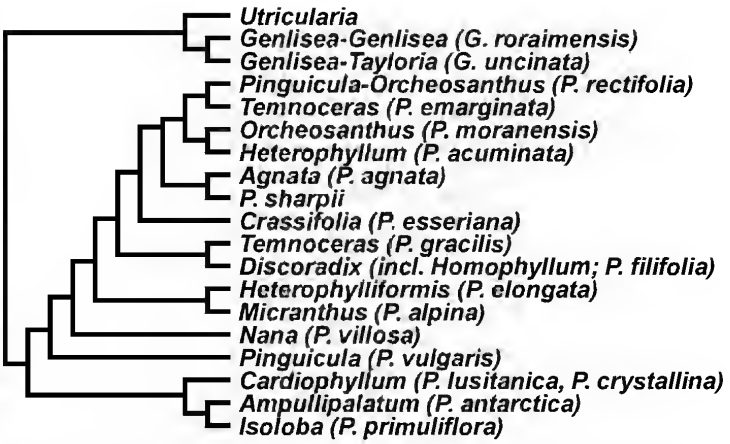


Figure 8: Phylogenetic tree of Lentibulariaceae showing detailed relationships within Pinguicula and Genlisea

The genus *Utricularia* (**215**) obviously emerged from a line closer to *Genlisea* probably after *Pinguicula* and *Genlisea* had diverged from each other. In fact, *Utricularia* can be deduced theoretically by neoteny from *Genlisea* (which in turn is also partially true for *Genlisea* from *Pinguicula*). The very elaborated suction traps of *Utricularia* constitute a ready and convincing means for generic separation. Being very probably the most derived and youngest genus of Lentibulariaceae, *Utricularia* shows a remarkable diversity of vegetative structure, trap (the mechanism remaining uniform), pollen and seed morphology, and capsule dehiscence, which allow grouping into sections, but which make natural phylogenetic arrangements rather difficult on the other hand (Taylor 1989). The origins of the nowadays very widespread genus (the largest of all carnivorous plants by species number and distribution) are somewhat obscure. The reduction of bracteoles at the base of the pedicels can be assumed to have occurred but once (with the notable exception of the otherwise obviously more primitive *U. heterosepala* - a doubtless member of sect. *Oligocista*) during the course of evolution within *Utricularia*, and it can be taken as a good marker for infrageneric classification. Thus, two large groups of sections can be defined. The more primitive ones share the presence of distinct bracteoles and predominance in tropical zones with *Genlisea*, the more derived and specialized ones lacking bracteoles constitute a younger group with (secondarily) wide distribution, comparable with the situation in subgen. *Pinguicula* of *Pinguicula*.

The essentially Australian (few species reaching New Caledonia and New Zealand) and closely interrelated sects. *Polypompholyx* (**2**), *Tridentaria* (**1**), and *Pleiochasia* (**33**) are commonly regarded as primitive (foliar organs more or less rosulate, flowers in pleiochasia, pollen 3-colporate with discrete endoapertures) although these do not meet geographically with any recent species of *Genlisea*, so it is not entirely clear if they actually are the phylogenetically oldest representatives of *Utricularia*.

A group of only little derived sections (*Australes* - **3**, Australian, *Meionula* - **3**, Australian and Asian, *Nigrescentes* - **3**, Australian, Asian, and African, and *Calpidisca* - **10**, Asian and African, only one species also disjunct in Mexico) can be assumed to be closely related to the foregoing group, showing similarities in trap structure and pollen morphology (in sect. *Nigrescentes*). *Meionula* and *Calpidisca* pollen structure (zonocolporate with 3 to 8 ectoapertures) approaches that of *Oligocista* and its allies *Benjaminia* and *Avesicarioides* (Lobreau-Callen *et al.* 1999).

The sections *Kamienskia* (**1**, China), *Phyllaria* (**13**, Asia, only one species also in Africa), and *Oliveria* (**1**, Africa and Madagascar) share dorsiventrally flattened pedicels and generally a reduced number of arms in the glands on the internal trap surface with sect. *Oligocista* (*v.i.*).

*Kamienskia* does also have a similar trap and bract/bracteole morphology. Its pollen is similar to that of *Oliveria* and *Oligocista*, whereas the pollen of *Phyllaria* is similar to that of *Stomoisia*. All three sections differ from *Oligocista* by the conspicuously unequal calyx lobes (the upper being larger). *Phyllaria* and *Oliveria* approach *Nigrescentes* by their basisolute bracts, apically extended placenta, and appendiculate seeds.

The section *Lloydia* (**1**, Asian, African, and American) is probably most closely related to *Calpidisca*, but with 7-10-colporate pollen it approaches sections *Psyllosperma* and *Foliosa* (*v.i.*), while its basisolute bracts are reminiscent of the more primitive sect. *Nigrescentes* (*v.s.*).

With its pronounced anterior trap appendage, sect. *Candollea* (1, east African) is apparently most closely related to sect. *Aranella* (**9**), which is apparently the most primitive section with a prevalence in the new world (only one species out of nine also reaching Africa). It is rather distinct in several features, including trap structure and fimbriate bracts and/or sepals. Sections *Aranella* and *Stylotheca* (*v.i.*) share zonocolporate pollen with 4 to 7 ectoapertures. The related but likewise distinct (filiform unicellular trap appendages) sect. *Martinia* (**1**) is restricted to South America.

By the number of species, a further large group of sections (*viz. Orchidioides* - **9**, *Iperua* - **5**, *Stomoisia* - **2**, *Stylotheca* - **1**, *Choristothecae* - **2**, *Benjaminia* - **1**, all American (one species of *Stomoisia* has recently also been discovered in west Africa), *Oligocista* - **37**, pantropical, *Chelidon* - **1** and *Avesicarioides* - **2**, African, and *Enskide* - **2**, tropical east Asian and north Australian) exhibits numerous features that appear plesiomorphic, but until their mutual relationships can be assessed more precisely, they are left at an intermediate position of the primitive infrageneric line with bracteoles (the only species that belongs here but lacks bracteoles, *U. heterosepala*, was already mentioned above). Some species (of *Chelidon*, *Orchidioides*, and *Iperua*) are adapted to epiphytic life with tubers as storage organs. All these share breviaxial pollen with sections *Stomoisia* and *Phyllaria* (*v.s.*), of which some species are interestingly likewise adapted to epiphytic or epilithic life. Sect. *Avesicarioides* is similar to *Oligocista* in all taxonomically relevant respects (bracteoles present, pedicels dorsiventrally flattened, pollen 4-6-colporate with narrow ectoaperture). Its adaptation to rheophytic habit causes superficial similarities to some more derived, likewise rheophytic American sections lacking bracteoles (*v.i.*), but these are obviously convergent and not due to a close phylogenetic relationship. Sect. *Choristothecae*, likewise composed of rheophytic species with bracteoles, displays similarities to the terrestrial Sect. *Stylotheca* (especially an elongation of the style not known in any other member of Lentibulariaceae), and it has 4-aperturate pollen (very distinct from the pollen with 8 or more ectoapertures found in the rheophytic species lacking bracteoles, *v.i.*), so sect. *Choristothecae* may represent a neotropical counterpart to *Avesicarioides* , demonstrating that rheophytic habit alone is obviously not a character defining only a single, monophyletic group in *Utricularia* (contrary to the opinion put forward in Taylor 1989).

The sects. *Psyllosperma* (**9**) and *Foliosa* (**3**), all American (predominantly tropical), exhibit a pollen type (8- or frequently more-colporate) that is characteristic for the group of sections uniformly lacking bracteoles (*v.i.*). This is especially noteworthy because in all representatives of sect. *Foliosa* and in some of sect. *Psyllosperma* the bracteoles are partially fused with their supporting bract, perhaps representing a transitional condition. On the other hand, trap morphology (with a densely glandular trap entrance) is very different from the species lacking bracteoles and rather reminiscent of the supposedly more primitive sections *Nigrescentes*, *Calpidisca*, and *Lloydia* (*v.s.*), of which only two widespread species (*U. livida* and *U. pubescens*, both with a comparatively high count of ectoapertures on their pollen) co-occur with *Psyllosperma* and *Foliosa* (in Central or Southern America, respectively). The latter two sections with their manifold relationships possibly represent a crucial (relictual?) intermediate stage in the evolution of the genus.

The more derived line of *Utricularia* that always lacks bracteoles and that is further characterized by subequiaxial zonocolporate pollen with 8 or more ectoapertures, is composed of principally two distinct groups. The first, apparently more primitive one (including sects. *Sprucea* - **1**, *Avesicaria* - **2**, *Mirabiles* - **2**, *Steyermarkia* - **2**, *Lecticula* - **2**, entirely American, *Setiscapella* - **9**, pantropical and subtropical, but predominantly American, and *Nelipus* - **3**, east Asian and north Australian) shares uniformly basisolute or tubular (in sect. *Lecticula*) bracts and terrestrial or rheophytic (*Avesicaria*, *Mirabiles*) habit with mostly undivided foliar organs. The sections *Avesicaria* and *Mirabiles* are further characterized by transversally flattened placentae

supported by a long stalk that originates from the ovary base, indicating mutual close affinities. The recent distribution pattern of sections lacking bracteoles (and their potential ancestors among sects. *Foliosa* and *Psyllosperma*, *v.s.*) strongly indicates an origin of their immediate common progenitor in (probably South) America, and subsequent waves of global range extensions in sects. *Setiscapella* (only few species outside America) and *Utricularia* (*v.i.*). The recent range of sect. *Nelipus* can possibly be explained by a comparatively recent origin (?from sect. *Setiscapella*), or alternatively by long-range dispersal and extinction in its original range (?America). Neither variant is entirely comforting, and further study is required.

The supposedly most advanced group (consisting of sects. *Utricularia* - **35**, almost cosmopolitan and *Vesiculina* - 3, American) consists of predominantly aquatic plants with much divided foliar organs and frequently freely suspended floating stems. Of the whole genus, only sect. *Utricularia* has reached wide distribution in the Holarctis. Three minute American species (*U. biovularioides*, *U. naviculata*, and *U. olivacea*) included in sect. *Utricularia* by Taylor (1989) are characterized by 7-10-colporate pollen (most of the remaining species in the section have 10-20-colporate pollen) and the lack of free-ending stolon segments (all segments are terminated by a trap), which may warrant segregation in a distinct section.

Until now, the scant caryological data on *Utricularia* are not conclusive (base numbers of x=7, 9, 10, and 11, only 28 species counted so far). Genetic data (rps16 and trnL-F, Jobson & Albert 2002; see Figure 9) support a basal position of sections *Polypompholyx* and *Pleiochasia*, sister to the remaining genus that is divided into two large clades roughly following the division according to bracteole reduction (with the exception of sections *Orchidioides* and *Iperua* that group as a sister clade to *Psyllosperma* and *Foliosa* rather than as a satellite of *Oligocista* as discussed above). The assumedly more primitive clade (bracteoles present, pollen with few apertures) has *Aranella* as sister to the remaining sections, compatible with a very primitive position as discussed above. A pair of clades, *viz. Phyllaria* + *Nigrescentes* and an unresolved group containing *Calpidisca*, *Australes*, and *Lloydia* is opposed to *Oligocista* and its allies (so far only *Benjaminia*, *Stomoisia*, and *Enskide* have been analyzed, so the picture is incomplete here). In the derived clade, the four sections *Orchidioides*, *Iperua*, *Psyllosperma*, and *Foliosa* form a common group that is sister to the bracteole-free sections. In these, the close affinity of *Avesicaria*, and *Setiscapella*, and a separation of *Biovularia* from the remainder of sect. *Utricularia* (and grouping *Biovularia* closer to *Vesiculina*) is supported.

References to all chromosome counts mentioned and a survey of all described taxa of carnivorous plants can be found on the World Wide Web (Schlauer & Walker 2000).

**Note:** This paper was presented at the 6th Conference of International Carnivorous Plant Society, June 1-5, 2006, Frostburg, Maryland, USA, and cannot reflect the most recent state of knowledge.

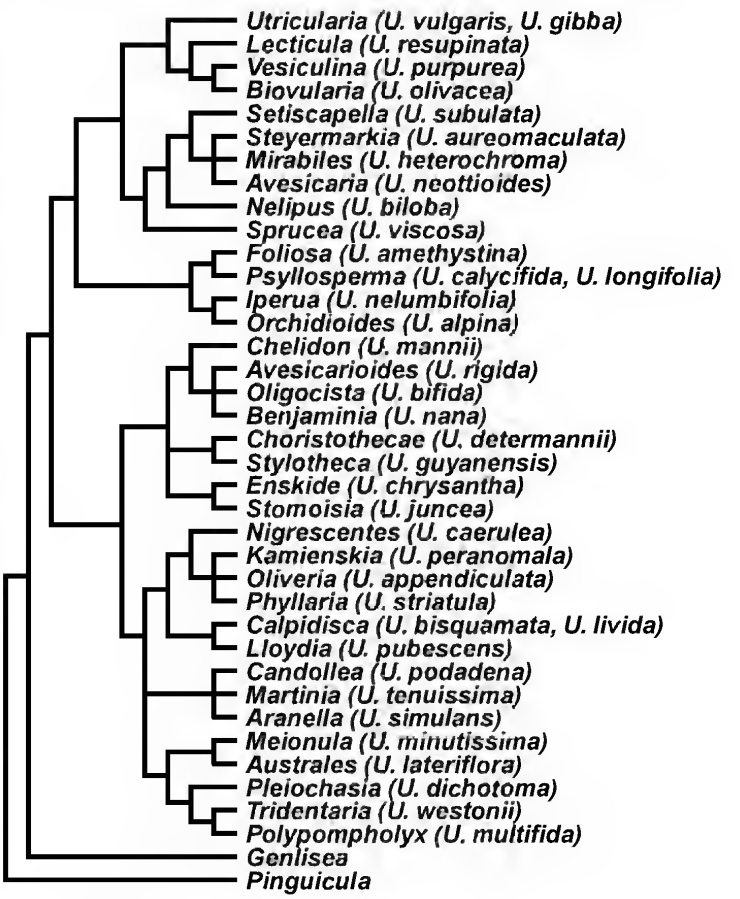

Figure 9: Phylogenetic tree of Utricularia

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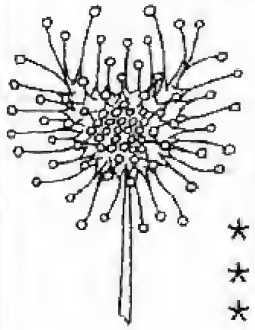

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## GROWING *HELIAMPHORA* INDOORS YEAR-ROUND.

BRIAN BARNES • brian@carnivorousplants.org
Keywords: Cultivation: *Heliamphora*, Terrarium, Lights

I am successfully growing the following *Heliamphora* indoors and thought I would share my experiences with the CPN readers.

*H. nutans*
*H. ionasii*
*H. sarraceniodes*
*H. hispida*
*H. heterodoxa* x *minor*
*H. elongata*
*H. follicularis*
*H. neblinae*

First, I highly recommend starting with one of the hybrids, such as *Heliamphora heterodoxa* x *minor*. It's a great, hardy plant that will teach a beginner some of the likes and dislikes of the genus, without costing you too much if it dies! Cooling for most species can be achieved by watering with lightly chilled water before you shut off the growlights and also ventilating with a small, low-power fan which can be purchased at any hydroponics shop. In my conditions, such species as *H. hispida*, *H. ionasii*, *H. neblinae* and *H. elongata* seem to require *more* of a nightly temperature drop than most other species and hybrids.

I set my grow tanks sideways with the opening to the front. This allows the lights to be placed on top of the glass to minimize heating during photoperiod. The glass is the perfect insulator for the bulbs and the light-spectrum is barely altered. This is allows you to bring your pitchers closer to the lights, with less risk of pitcher burn. A constant, light breeze is VERY important if your pitcher tops are within a few inches of the bulbs, even with the glass between them. I prefer my pitchers to be about 10 cm (4 in) from from the glass/bulbs. This safely gives the plants superb coloration, combined with good size and pitcher form. This also allows for the light breezes from the fan to enter the front and circulate throughout the chamber. Currently, I run two chambers, a 375 l (100 gal) and a 285 l (75 gal) aquarium as such, with a total of twelve 40 watt Agri-Sun tubes, on a 14 hr photoperiod. In winter, I reduce the photoperiod to 11 hrs for three months, since average indoor temperature is naturally kept 5-8°C (10-15°F) degrees cooler than in summer. By doing so, I have now given my *Heliamphora* a winter...or so they think!

This practice seems to induce flowering in my mature plants. Very importantly, I make sure my plants are placed high in their pots of pure living Florida *Sphagnum* moss. The media surface should not be below the rim's edge. This practice allows for some evaporative cooling to take place during the day and most importantly at night. Try to be careful and exercise care when working in the chamber. There's no feeling like snagging and breaking a perfectly formed nectar spoon from a huge *Heliamphora follicularis* pitcher, two days before it even opens!

Here's my daily summer and winter regime for year-round *Heliamphora* cultivation indoors. Keep in mind that I live in Florida, which is tropical and everyones growing conditions are different, but this method should work for anyone who keeps their grow rooms about the same temperatures as mine. Never be afraid to experiment to find what works best for you.

Winter- 11 hr photoperiod. First misting with pure RO water when lights first come on. Fan runs constantly while lights are on and off, but fan shuts off for 2 hrs prior to photoperiod beginning, to allow for humidity to build in chamber. This mimics the dew or fog that usually occurs prior to sunrise *in situ*. Since the humidity in winter is much lower inside and outside, I mist four times daily in winter, every 2 1/2 to 3 hrs whenever possible. This gives me a constant humidity level of 60 to 65 percent.

Proper air circulation is a must and can be monitored. Excellent wind vanes can be made by using a 15 cm (6 in) long, 6 mm (1/4 in) wide piece of reflective Mylar taped near the center, 15 cm (6 in) away from each end of the chamber. You want to see the Mylar strips moving at all

times. Plants are then watered with lightly chilled RO water around the outside edges of the pots to avoid too much shock to the roots. Too much of a temperature drop at one time, and may shock your plants. My patio serves as a perfect natural cooler during our mild Florida winters.

I like my water temperature to be around 15°C (59°F). And so do my plants. The main challenge is getting your pots and media to cool at night. If your plant's pots are cool at night, then naturally your chamber will cool some also via evaporative cooling. I call the mounded plantings "The Wicking Effect", due to the ability of the breeze to partially pass throughout the top of the media, thus sustaining chilled water deep down in the pot, for a longer period.

To change seasonal photoperiod times, increase or decrease lighting by one hour increments over a three week period. During winter, temperatures are 18-20°C (64-68°F) at night and 25-27°C (77-80°F) by day (with an 11 hr photoperiod). Humidity is 60-65% constantly, fluctuating up to 70-75% after misting plants and chamber. Misting is done four times daily to compensate for lack of humidity indoors. Watered with lightly-chilled RO water prior to "lights out" until pots drip. Constant air circulation 22 hrs a day.

Fan clicks off for two hours via timer to simulate sunrise. During summer, temperatures are 22-23°C (71-73°F) at night, 27-28°C (80-82°F) by day (with a 14 hr photoperiod). Humidity is 70-75%, fluctuating up to 85-90% after misting. Misting only needed three times a day due to increased indoor humidity. Water pots until dripping with lightly-chilled RO water prior to "lights out". Note: During Summer, on Tuesdays and Fridays, I only run half of the lights in the chambers for 14 hrs to mimic the cloudier/lower spectrum days *Heliamphora* would experience *in situ*. Misting is doubled during these days to mimic rainy, wetter conditions.

And, there you go! I hope that this article helps some growers to successfully cultivate this most seductive and beautiful genus.

Figure 1:
*Heliamphora* tank setup

Figure 2:
A happy *Heliamphora follic-ulata*

# THE SAVAGE GARDEN:
## "By the light of the silvery moon"

Peter D'Amato • California Carnivores • 2833 Old Gravenstein Hwy • Sebastopol, CA 95472 • USA • califcarn@aol.com

Keywords: Cultivation

Imagine this. You are in southern Alabama. It is a warm night, the sun having set in a dying blaze of orange and red a few hours before. You are standing on a grassy slope overlooking a wet meadow of white trumpet plants, *Sarracenia leucophylla*. It is early October, and the sound of a chorus of crickets and tree frogs reverberates against the stands of longleaf pines (*Pinus palustris*) that surround much of the open meadow. To the east, just over drooping fronds of some scattered cabbage palms (*Sabal palmetto*), hangs the moon. It is full, some call it the harvest moon in early autumn, and it really does look larger than normal, an optical illusion they say, big, bright and silvery. The light is so bright, the cabbage palms and pines form distinctive shadows over the edge of the dense stand of white trumpets - thousands of them bathed in the light of the silvery moon. The trumpets catch the glow. It almost seems as though candles are within each pitcher tube, the whiteness of the pitchers reflecting the moonlight. If you focus your eyes, you can see the dancing movement of tiny black specks and blotches along the mouths and lids of the trumpet plants. They are moths and other nocturnal insects, like bugs fluttering around a light bulb at night.

We will return to our moon-lit meadow of white trumpets momentarily. But first let us talk of other things. Let us ponder some of the more unusual physical adaptations of carnivorous plants, particularly some surprising discoveries in the past one or two decades. While for nearly 140 years carnivorous plants have been known to lure, catch, kill, and feed upon insects by various treacherous traps and trickery, there have been some amazing discoveries made concerning how specialized a few species have become in their quest of nutrients usually absent in the soils in which they grow. Often, these adaptations concerned peculiar physical properties of the plants that were mysterious, yet unexplained.

It was around twenty years ago that Cliff Dodd, a grower in Florida, and I noticed almost simultaneously that our *Nepenthes lowii* plants were doing something unusual. He and I had probably the only sizable plants of this species in cultivation in America at the time. We both noticed an oozy, white, bead-like substance appearing among the bristles that hung from the inner surface of the lid. This surprised us, since we had read that these white clusters had been seen on the plants in the wild. They were assumed to be snail or slug eggs, laid there for the protection of the hopeful offspring, a reasonable assumption at the time. However here it was on Cliff's and my cultivated plants. I nicknamed the stuff "smegmata".

It wasn't until Charles Clark made the astounding revelation in his 1997 "Nepenthes of Borneo" that according to his field observations, this white substance lured small birds that fed on the smegmata, dropping their feces into the wide, flared upper pitchers of *N. lowii*, making the plant a "crapivore", as I have often joked in my lectures, or, more coarsely, "sh**ivorous". *N. ephippeata* has evolved a similar adaptation.

*Nepenthes albomarginata* was a widely grown plant as the hobby grew in the 1990s, and all of us admired the distinctive white band on the pitcher, just below the peristome. Why was it there? Some visual lure for insects, no doubt.

But it wasn't until the recent turn of the century that ecologists Jonathan Moran, Marlis Merbach and their associates discovered the true nature of this white band. It was covered in minute, hair-like trichomes that a specific species of termite found irresistible. The termites would swarm over the white band eating the hairs, hundreds to thousands of the insects being caught by the pitchers in the course of one night. Most interesting is that the peristome had to be stumbled upon accidentally by one or a few termites, who would then return to the nest to notify the colony of a tasty food source. Remember, this band is bright white. The termites are nocturnal. It was not mentioned by its discoverers if the moon was full.

One drawback to more discoveries of this sort is that one has to be there to observe it, in the wild, where it occurs. We would never have known about the true nature of the white band of

*N. albomarginata* or the smegmata of *N. lowii* if we had only studied cultivated plants.

Another astounding discovery was by Siegfried and Irmgard Hartmeyer concerning the species of sundew they discovered, named *Drosera hartmeyerorum*. In Stewart McPherson's book "Glistening Carnivores", he offers a detailed report by the Hartmeyers - and amazing photos - of the truly weird tentacles found near the base of the leaves that are topped with bizarre reflective lenses. These lenses catch sunlight and "glow", possibly as a lure to insects. In "Glistening Carnivores" there is even a photo of these reflective lenses illuminated in the dark by a torch or flashlight. Would moonlight reflect in these lenses, visible to nocturnal insects in ways that human eyes could not see?

Not all of the above examples pertain to moonlight in particular, such as the smegmata on *N. lowii*, although it is opaque to white in color. My point is that there are some curious physical adaptations of some carnivorous plants that are unexplained and should arouse our curiosity and study.

One example is the unusual "eye spots" found in most - but not all - *N. reinwardtiana* pitchers. These two small circular spots are typically on the inner back wall of the interior of the pitcher. Similar spots are sometimes found in other species, such as *N. mikei*, *sanguinea*, and *tobaica*. These eye spots lack the wax of the rest of the pitcher interior. Do they have a specific purpose? Experience with such oddities suggests that they probably do.

However *N. khasiana* usually has a distinctive red band below its peristome, but since red is produced by anthocyanin, known to cause color appealing to the ultraviolet spectrum of light that insect eyes are particularly adapted to, we may assume the color is a typical visual lure, hinting to insects where the nectar is to be found. Insect eyes are very different than ours and many plants, especially their flowers, control insect behavior by color patterns as well as scents.

But let us return to our meadow of white trumpets under the harvest moon.

Don Schnell, in his book "Carnivorous Plants of the United States and Canada", points out something we all now commonly know. *Sarracenia leucophylla* produces its largest, most robust trumpets late in the season, in late summer and autumn, "as though the growing season were starting again, but, of course, the time for frost is nearly at hand." He also states: "...this flush of late summer pitchers is peculiar to *S. leucophylla*."

Could it be merely coincidence that this beautiful species, nearly pure white, produces its best leaves during the haunting brightness of the harvest moon?

This idea did not originate with me. In 1997, I gave a presentation at the North Carolina Botanical Gardens, and one fellow told me a fascinating story. He was in a stand of white trumpets during the bright autumn moon. He said they seemed to glow in the dark. He was especially impressed with the observation that they were catching an abundant quantity of moths. He believed the moths were of one species, and even suspected they were of a particular sex. He wondered if the sweet, musty odor the pitchers produced imitated pheromones that lured either one sex of the moth or the other.

Even though I have kept a daily journal of my life for 38 years, and recorded many details of that trip and the people I met there, I neglected to record the name of the person who told me that story! However, I recently contacted long-time *Sarracenia* enthusiast Randy Troup, who I met at that presentation. He told me the late Rob Gardiner, director of the North Carolina Botanical Gardens for many years, and for a while a co-editor of this newsletter, used to talk about white trumpets and moonlight to him. Since I went on a memorable field trip on that visit with Rob and Larry Mellichamp, it's quite likely Rob was the source of this idea.

Although moonlight has only 1/50,000 the intensity of the sun, many plants have adaptations to the light of the moon. Some flowers bloom only in moonlight. Some plants "block" moonlight so it doesn't interfere with normal photoperiodism of the sun. Lunar biorhythms affect not only animals but plants. Some people grow "moon gardens", which contain plants that have leaves that are white or pale in color. A Google search under "plants moonlight" will bring up a vast array of information.

If *S. leucophylla* has adapted to make use of the light of the silvery moon, then what about the light windows of *S. minor* or *Darlingtonia californica*? Obviously they are most effective in the sun. But since so many insects are nocturnal, could they also "work" in moonlight?

What about the *Nepenthes*, most often richly colored in reds and purples in their lower pitchers, while the upper pitchers, climbing into the sunlight or moonlight, are most often pale green,

and some, like *N. muluensis*, having bright white lids?

Patrick Hollingsworth, a friend and volunteer at California Carnivores, has been taking incredible photographs of *Utricularia* traps using a high-powered microscope. He says many of the tiny traps of aquatic species reflect light and "shine", even when dimly lit by a nearby table lamp.

And what about the glittering leaves of sundews? To the eyes of nocturnal insects, might they be called....moondews?

One thing we must remember. Moonlight is sunlight, reflected by our lunar companion. Although night time varies on our earth according to latitude and seasons, plants live in moonlight as much as the direct rays of the sun. That some carnivorous plants may take advantage of the moon's silvery glow is not out of the realm of possibilities.

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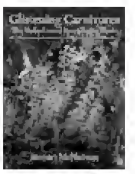

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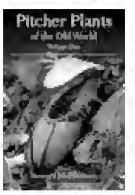


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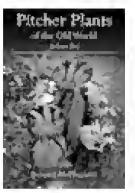


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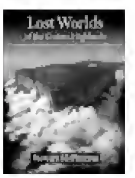


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